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ENERGY BUDGETS IN FREE-LIVING GREEN IGUANAS IN A SEASONAL ENVIRONMENT[1]

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Abstract. Using a variety of techniques we estimated energy expenditure and allocation of energy in free-living green iguanas (*Iguana iguana*) in a seasonal environment on Curaçao, Netherlands Antilles.

1) Daily energy expenditure (DEE) was measured by means of the doubly labeled water (DLW) technique, using ^{18}O and deuterium (^{2}H). The method was validated in green iguanas at ambient temperature and humidity levels occurring on Curaçao. Energy expenditures from the DLW method differed by 2.1 ± 8.2% compared to respirometry and balance methods. This value falls within the range of deviations found in other validation studies, and indicates that the DLW method is acceptable in green iguanas even at high ambient humidity.

2) Average DEE was 71.7 $kJ \cdot kg^{-1} \cdot d^{-1}$. There were no significant differences in DEE between males and females, although males tended to have higher metabolic rates during the mating season. Energy expenditure on a yearly basis including clutch production in females did not differ between females and males, indicating comparable annual levels of energy expenditure between the sexes.

3) Temperature dependence of standard metabolic rate (SMR) and resting metabolic rate (RMR) were determined by respirometry experiments. RMR increased with temperature with a Q_{10} of 2.24. In combination with field body temperatures SMR and RMR of free-living iguanas could be determined. SMR amounted to 15–22% of the DEE. DEE was 1.8–2.8 times RMR.

4) The energy expenditure above RMR was allocated between activities involving locomotion and stationary activities. DEE in combination with behavioral data revealed an indirect measure of the costs linked to locomotion in the field, including climbing (255 $kJ \cdot km^{-1} \cdot kg^{-1}$). Locomotion with a climbing component imposed six times the costs of horizontal walking. Although time spent locomoting was only a very small fraction of the total time, the costs linked to locomotor activities amounted to ≈23% of the daily energy expenditure. Postural adjustment costs were ≈33% of the DEE. Locomotion could explain 78% of the observed variation in DEE. If other activities, such as foraging and social activities, were included in multiple regression analyses, 96% of the variation in DEE could be explained.

5) Body condition of males decreased during the mating period (March/April), while most of the decrease in body condition of females occurred during the time of oviposition (May/June). Time spent in social activities was higher during the mating period, especially so in males, but time devoted to other activities (locomotion, foraging) did not differ significantly between the seasons. Comparison between the sexes revealed that males spent more time locomoting than females, throughout the year.

6) Differences in body condition in the course of the year were not due to differences in DEE, but were mainly a result of differences in metabolizable energy intake. Though on a yearly basis energy expenditure was equal in both sexes, energy allocation differed between the sexes. Females devoted ≈15% of their annual energy budget to the production of eggs, while males showed heightened social activity during the mating phase and spent twice as much time in locomotor activities than females.

Key words: condition index; DEE; doubly labeled water; energetics; energy allocation; energy budget; FMR; herbivorous lizard; Iguana iguana; *respirometry; RMR; SMR.*

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Introduction

A fundamental problem in the study of the ecology and behavior of individual organisms is how they allocate resources. For example, the central concept of life history theory is that resources retained for future reproduction, growth, or maintenance are not available for any of the other functions. Therefore, to understand the biology of an organism in nature, an accurate analysis of the energy budget is necessary. An individual's energy budget must be governed by a complex set of conditional rules that are molded by natural selection to maximize reproductive success. The daily energy expenditure (DEE) could vary depending on (among other things) resource availability, environmental conditions, and reproductive state. The ultimate goal of energy budget studies is to understand the way energy is allocated to different activities such as foraging, food utilization, territorial defense, courtship, mating, and production of offspring. Here we examine the energy budget of the herbivorous green iguana (*Iguana iguana*) in the strongly seasonal environment of Curaçao, Netherlands Antilles. Since the green iguana is a seasonal breeder, the demands for resources are also expected to vary with seasons and will be affected by sex. Therefore a comparison is made between energy budgets of male and female iguanas, and between the mating season and the nonmating season.

Several studies on energy budgets of lizards have used the doubly labeled water (DLW) technique (Lifson and McClintock 1966, Nagy 1980), yielding estimates of energy expenditure in free-living lizards. Most DLW studies do not provide detailed descriptions of the way energy is allocated to different activities, and food intake was not measured independently. In many DLW studies food intake was estimated from water flux, which is not independent from the final DEE estimate itself. Assumptions made to estimate food intake include: (1) Body water changes during period of measurements are proportional to body mass changes (Nagy 1975, Mautz and Nagy 1987, Anderson and Karasov 1981), or animals are assumed to be in energy balance (Nagy and Shoemaker 1984). (2) No water other than dietary water enters the animal (Nagy and Costa 1980). (3) The proportion of the food items in the diet can be estimated from stomach contents of other individuals than those selected for the DLW measurements (Nagy and Shoemaker 1984, Mautz and Nagy 1987, Anderson and Karasov 1988), or from the stomach contents of focal animals at the end of the experiment (Nagy et al. 1984).

Though the above-mentioned assumptions may be valid in some animal studies, they are a potential source of error in others, especially if intra- or inter-individual variation in food or water intake is high. We therefore combined four methods to measure energy expenditure and allocation in free-ranging green iguanas in different phases of the annual cycle: (1) daily energy expenditure was measured using the DLW method; (2) time budgets were constructed from continuous observations; (3) field body temperatures in combination with calorimetry experiments were used to estimate resting metabolic rate (RMR) and standard metabolic rate (SMR) in the field; (4) metabolizable energy intake was obtained from direct observations of food intake, chemical analyses of food, and digestion trials, and was compared with body mass changes.

Previous DLW studies of reptiles used ^{18}O- and tritium-labeled water. Here we use for the first time deuterium instead of tritium. Though deuterium has been used successfully in studies on energy budgets in birds (Masman and Klaassen 1987) and humans (Westerterp et al. 1989), it has never been used in reptile studies. Two studies report a validation of the DLW method in lizards, using ^{18}O and tritium (Congdon et al. 1978, Nagy 1983*a*). However, no validation using tropical lizards has been described. Furthermore, previous validations use dry air in respirometer chambers. High ambient humidity, as exists on Curaçao, can cause large errors due to water influx through skin and lungs (Nagy 1980). We carried out a validation study under the same humidity conditions as met on Curaçao.

Methods

Study site

The field work was carried out in the area of the former Sta. Barbara estate on Curaçao, Netherlands Antilles. The study site encompassed ≈0.65 ha with large limestone boulders situated in front of a limestone plateau. The iguanas lived mainly on these boulders, where they found shelter and basking places. They foraged in the vegetation surrounding the rocks. Each large boulder was inhabited by small groups of iguanas, consisting of a dominant male, 1–4 females, on some rocks a subordinate male, and several yearlings.

Curaçao has a semi-arid climate with strong spatial and seasonal variation in rainfall. Mean annual rainfall amounts to 570 mm, to which the rains in October–January contribute 64%, although much variation occurs from year to year. Monthly mean air temperature is 27.5°C, with minimum and maximum mean temperatures of 25.3°C in January and of 30.9°C in September. Mean monthly relative humidity is 77 ± 1%. From the northeast, strong trade winds blow nearly all year round (mean: 7.1 m/s). Daylight is available from 11½ hours (0700–1830) in January to 12¾ hours (0610–1900) in June.

The iguanas show a distinct reproductive cycle where courtship and mating take place in the first half of the dry season (March, April), followed by the period of oviposition in the end of April and May (van Marken Lichtenbelt and Albers 1993). In this study we will compare data from adult males and females on time and energy budgets between the mating period and the rest of the year. Measurements on female budgets during the time of egg-laying were not included.

TABLE 1. Comparison of CO_2 production in green iguanas (*Iguana iguana*) as measured by the doubly labeled water method (DLW), respirometry method, and from metabolizable energy intake (MEI) at constant body mass (BM) (Balance).

Exp.	Sex	Mean body mass (g)	ΔBM (g/d)	Temperature (°C) Day	Temperature (°C) Night	Rel. humidity (%)	Time (days)	CO_2 production ($mL \cdot g^{-1} \cdot h^{-1}$) DLW	Respirometry	Balance	Error (%)
V1	♀	981	−15.92	30	30	50–60	12.4	0.081	0.081	···	0.0
V2	♀	562	−5.83	30	30	50–60	12.4	0.094	0.097	···	−3.1
V3	♂	521	−7.29	35	35	60–70	7.2	0.168	0.163	···	+2.9
V4	♂	1079	−0.20	37	35	60–70	20.2	0.171	0.153	···	+11.8
										Mean ± 1 SD	2.9 ± 6.4
V5	♂	1042	−1.37	35	30	65–85	27.6	0.094	···	0.103	−9.6
V6	♂	1039	−0.85	35	30	65–85	27.6	0.123	···	0.110	+10.5
										Total mean ± 1 SD	2.1 ± 8.2

Doubly labeled water measurements

DLW procedures.—^2H and ^{18}O were used to measure CO_2 production (Lifson and McClintock 1966, Nagy 1980, Masman and Klaassen 1987) in free-living green iguanas. The animals were caught with traps in the daytime (two animals) or by night from their sleeping places. Upon capture they were weighed and their body length (snout–vent length: SVL) was measured. A 25-μL blood sample for determination of the normal isotopic abundance (background) was taken by extraction with a heparinized capillary tube inserted into the post-orbital sinus. The iguanas were injected intra-peritoneally with a mixture of ^{18}O and ^2H. The amount injected was 0.6 g ^{18}O (50.23 atom%) and 0.15 g ^2H (99.8 atom%) per kilogram body mass in the first two experiments and 0.9 g ^{18}O (50.23 atom%) or 0.45 g ^{18}O (90.02 atom%) and 0.25 g ^2H (99.8 atom%) in the other experiments. After 12–19 h the initial blood sample was taken (the equilibrium time of isotopes in the body water was 12 h, determined on three iguanas in the laboratory from which blood samples were taken at 2-h intervals). Immediately after sampling, the animal was released at the place of capture. The iguanas were recaptured after 12–25 d (exception Exp. 8: 37 d). Body mass was determined again and a final blood sample was taken. Analyses of the blood samples (taken in duplicate) were carried out according to the procedures described in Masman and Klaassen (1987). A total of 17 successful experiments were carried out. During four experiments the animals were followed continuously. In five other experiments the animals were followed for at least 6 d. No DLW measurements were taken from gravid females in the last 2 mo before egg-laying.

CO_2 production was calculated using corrections for fractionation (Eq. 35 in Lifson and McClintock 1966). Body water volumes were determined by calculating the dilution space for the injected ^{18}O molecules, from the enrichment of the first sample after injection (Schoeller et al. 1980). Carbon dioxide production was converted to energy expenditure using an RQ of 0.92 (Nagy 1983*b*).

Validation of the DLW-method.—The DLW-method using deuterium was validated for iguanas under ambient humidity and field body temperature as found on Curaçao. Mean relative humidity on Curaçao is 77% at a mean ambient temperature of 25.7°C, resulting in high ambient humidity of 2.82 kPa. To validate the method the DLW technique was used simultaneously with two other methods.

1) CO_2 production of resting iguanas was measured using both DLW and infrared gas analysis (IRGA) in four animals by respirometry in the Netherlands at the State University of Utrecht (experiment V1 and V2) and the State University of Groningen (experiment V3 and V4). Respiration chambers of 0.40 × 0.48 × 0.20 m (V1 and V2), 0.40 × 0.30 × 0.25 m (V3) and 0.50 × 0.40 × 0.35 m (V4) were used, through which ambient air was led. The air flow was measured and the difference in CO_2 and O_2 concentrations between ambient and outgoing air were obtained, using a Hereaus CO_2 meter and a Servomex Taylor oxygen meter (V1 and V2), and a Binos CO_2 meter and a model S3A Applied Electrochemistry oxygen meter in the experiments V3 and V4. CO_2 production was calculated after Hill (1972). Because in experiment V3 no oxygen consumption was measured, for the calculation of the CO_2 production an RQ of 0.9 (average value found in the other experiments) was used. The respiration chambers were placed in constant-temperature cabinets. Air humidity (Table 1) could be adjusted by flowing the air through a bottle with water in a thermally controlled water bath. The experiments lasted 1–3 wk (Table 1). The animals were taken out of the respiration chamber every 2 d for 5–15 min and fed lettuce and bananas. It was assumed that the CO_2 production and O_2 consumption during the time outside the chambers was 1.5 times the average measured values. In experiments V3 and V4 lacrymal fluid samples were taken for the DLW measurements, which can be used instead of blood (Nagy 1983*b*). Because during these experiments the equilibrium time was not yet known, the CO_2 production was calculated using the theoretical initial enrichment with ^2H and ^{18}O and a body water percentage (BW%) of 70% (mean 70.1 ± 1.8%, obtained from eight desiccated animals). The theoretical ^2H dilution space

was corrected by dividing by 1.051, since the ^2H dilution space in our experiments was on average 5.1% larger than the ^{18}O dilution space.

2) On Curaçao at the Carmabi Institute energy expenditure was determined using the DLW technique together with a feeding trial in two iguanas (experiments V5 and V6). Amount of food (leaves of *Ipomoea batatas*) intake, and feces and uric acid production, were determined. Both food and excreta were dried at 50°C, and analyzed for nitrogen (Kjeldahl method) and energy content (Parr adiabatic bomb calorimeter; more details on the experimental setup are presented in van Marken Lichtenbelt (1992)). From these data the metabolizable energy intake (MEI) could be calculated. MEI was presumed to be equal to energy expenditure, assuming that the animals maintained constant body mass (although they lost some body mass, Table 1) and that no deposition and mobilization of body fat occurred. CO_2 production was calculated using an RQ of 0.92.

Time budgets

Animals on the site were caught with traps in daytime or by night from their sleeping places. The number of captures was limited in order to reduce disturbance of the animals. They were sexed and body mass and snout–vent length were determined. Upon release they were color-marked with glass beads sewn on the dorsal crest. Iguanas were studied by observation through telescopes and binoculars by 2–3 persons who communicated by radio. From blinds surrounding the observation rocks the iguanas could be followed continuously. Because the iguanas tended to forage in the top layer of the trees, even the behavior of animals in the vegetation could be observed in detail. The animals could be recognized by colored glass beads or by individual characteristics on tail, dewlap, and crest. Observations took place from local sunrise (½ h after sunrise) until sunset. Individuals were followed on a daily basis. Complete days are those in which an animal is followed continuously throughout the day and bites could be recorded for >90% of the total foraging time. For comparison between behavioral data, only results of those animals for which at least three complete days were available were used.

The following data from the animals under observation relevant to time budget were registered *every 5 min*: (1) the animal's location, from which the covered distance could be determined for each time interval; (2) movement since the last 5-min record: a distinction was made between a change in position (movement ≤30 cm), and change of location (movement >30 cm); (3) locomotor activities: walking on the rock, sprinting, drinking.

At 5-min intervals the animal's behavior was recorded continuously during *1 min*. Recorded were: (1) locomotor activity: number of steps; (2) interactions: number of bobs (stereotyped head-nodding in series, Distel and Veazey 1982), time spent on social activities, i.e., hierarchy setting, copulations, copulation attempts, fighting, chasing. Data on grazing of animals were taken on a *minute to minute basis*. During each minute the number of bites, steps, and bobs were recorded. A meal is defined as the period in which the animal is foraging without an interruption of >30 min. Foraging time is defined as the sum of those minutes in which grazing actually occurred.

Standard and resting metabolic rate

Temperature dependence of standard metabolic rate (SMR) and resting metabolic rate (RMR) was determined in five iguanas (body mass: 530–1165 g). SMR is the energy expenditure of fasting animals in the dark in the inactive phase of their diurnal cycle (Bennett and Dawson 1976). RMR is measured under the same circumstances under nonfasting conditions. The animals were housed in 1.5 × 1 × 1 m terraria with 12 h light–dark cycle (0700–1900) and fed lettuce, fruits, and some cat food. Prior to the RMR experiments only lettuce was offered during 1 wk. Food was withdrawn for 6 d before the SMR experiments started. Passage time of readily digestible food was 5 d (van Marken Lichtenbelt 1992).

SMR and RMR were determined at body temperatures ranging from 29° to 37°C by measuring O_2 consumption and in some cases also CO_2 production. Mean field body temperatures range from 27°–29°C (night) to 31°–36°C (day) (van Marken Lichtenbelt 1991). Experimental location and procedure was as described above for validation of the DLW method in experiments V3 and V4. During the experiments the light : dark cycle was 12:12. A thermistor was inserted at least 3 cm into the animal's cloaca. The animals were put in the respirometer in the late afternoon or early evening for 24 h. Metabolism reached the lowest (stable) values after 0200. SMR and RMR were obtained from average O_2 consumption during 0300–0700.

Field SMR and RMR were calculated from field body temperatures (T_b, determined every 15 min) and the relations between T_b and RMR and SMR. Temperature telemetry or a temperature simulation model was used to determine body temperatures of free-living iguanas (van Marken Lichtenbelt 1991).

Metabolizable energy intake

Daily metabolizable energy intake (MEI) was calculated from direct observations (van Marken Lichtenbelt 1991). During foraging all bites were registered and bite sizes (grams of dry matter) were afterwards estimated by sampling, drying, and weighing plant items of the same sizes as were grazed by the animals. Digestibilities of several food items were determined in a series of digestibility trials (van Marken Lichtenbelt 1992). From these data the MEI could be calculated; possible energy loss with H_2 and/or CH_4 was neglected. For comparison of MEI and DEE a selection was made

TABLE 2. Daily energy expenditure (DEE) determined by the DLW method, mean body mass (BM), and BM change in free-living green iguanas.

Period	Exp.	Animal	Sex	BM (g)	ΔBM (g/d)	DEE (kJ/d)	DEE ($kJ \cdot kg^{-1} \cdot d^{-1}$)
Nonmating period							
May, Jun 1987	1	RN	♂	702	0.2	45.7	65.1
May, Jun 1987	2	RB	♂	552	1.6	48.1	87.2
Sep, Aug 1987	3	LB	♀	787	−0.3	65.5	83.2
Sep, Aug 1987	4	YB	♂	1305	−1.6	76.0	58.2
Sep, Aug 1987	5	BY	♀	975	−2.3	72.3	74.2
Sep, Aug 1987	6	GO	♀	1328	0.3	73.9	55.6
Sep, Aug 1987	7	LY	♂	1012	−0.2	71.5	70.7
Dec, Jan 1987, 1988	8	OO	♀	782	−1.7	60.8	77.8
Dec, Jan 1987, 1988	9	BY	♀	1000	−1.4	59.5	59.5
Dec, Jan 1987, 1988	10	BG	♀	902	−4.4	57.8	64.1
Dec, Jan 1987, 1988	11	PB	♂	787	−0.7	59.0	75.0
Mating period							
Mar, Apr 1988	12	LLa	♀	783	−4.6	51.6	65.9
Mar, Apr 1988	13	LLb	♀	712	−3.6	55.5	77.9
Mar, Apr 1988	15	PB	♂	628	−5.8	53.8	85.7
Mar, Apr 1988	16	LB	♂	695	−5.1	53.5	77.0
Mar, Apr 1988	17	LY	♂	815	−8.5	57.1	70.1

	DEE Mean ± 1 SD (*n*)
Nonmating period	
Males	71.2 ± 10.9 (5)
Females	69.1 ± 10.9 (6)
Mating period	
Males	77.6 ± 7.8 (3)
Females	71.9 ± 8.5 (2)

of animals for which at least six complete observation days were available, within the period of the DLW experiments.

Clutch size and shedding

Clutch mass (CM) in the green iguanas is closely related to gravid female body mass (CM = 0.32BM − 4.3; $r = 0.89$; $P < .005$; $n = 68$; van Marken Lichtenbelt and Albers 1993). This relation was used to estimate clutch mass for calculation of energy investment in reproduction in females. Twelve eggs from different clutches were weighed and dried at 50°C to determine dry matter content. Energy content of yolk (including albumen) was measured using an adiabatic bomb calorimeter (Parr), and protein content was determined by the Kjeldahl method.

Shedding condition of the green iguanas was recorded during observations and from captured animals. In order to obtain an estimate of the energy investments of shedding, skin lost during shedding was collected from captive animals. Shed skins were dried and analyzed for energy content, according to the procedure described above.

Statistical analyses

Numerical results throughout the text are given as mean ± 1 SD; in some cases standard error of the mean is specified. The *t* test was used to compare means between groups. Analyses of covariance (ANCOVA: Sokal and Rohlf 1981) were used to compare the slopes and intercepts of linear regressions.

RESULTS

Validation of the DLW method

The mean deviation of the CO_2 production measured by the DLW method and (1) the gas analyses in a respirometry apparatus and (2) the MEI at constant body mass experiment was 2.1 ± 8.2% (Table 1). Thus CO_2 production measured with the DLW method, using D_2O and $H_2{}^{18}O$, even under high air humidity circumstances, is as accurate as in other reptile, mammal, and bird studies. This method can thus be used for estimation of daily energy expenditure in free-living green iguanas on Curaçao.

Daily energy expenditure

Mean daily energy expenditure was 71.7 ± 9.7 $kJ \cdot kg^{-1} \cdot d^{-1}$ (Table 2). There were no significant differences between males and females, combined for all periods. In the mating season, however, mean DEE tended to be higher in males (77.6 $kJ \cdot kg^{-1} \cdot d^{-1}$) than in females (71.9 $kJ \cdot kg^{-1} \cdot d^{-1}$), but the number of measurements was low. Field energy metabolism for the green iguanas studied can be described by the allometric equation:

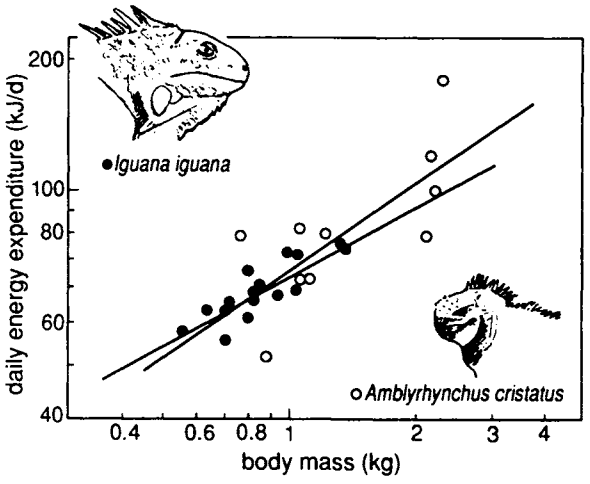

FIG. 1. Relation between daily energy expenditure (DEE) and body mass (BM) in the green iguana (*Iguana iguana*) on Curaçao, and in the Galápagos marine iguana (*Amblyrhynchus cristatus*) (data from Nagy and Shoemaker 1984). Equations: *I. iguana*: $DEE = 64.9BM^{0.53}$; $r = 0.85$; $P < .001$ ($n = 16$); *A. cristatus*: $DEE = 66.9BM^{0.68}$; $r = 0.74$, $P < .05$ ($n = 10$); both species combined: $DEE = 66.71BM^{0.65}$; $r = 0.82$; $P < .01$ ($n = 26$).

$$DEE = 64.9BM^{0.53}\ kJ/d$$
$$(r = 0.85,\ P < .001),$$

where BM is body mass in kilograms (Fig. 1). The logarithmic equations for males and females were not significantly different (ANCOVA: slopes: $P > .75$, intercepts: $P > .25$).

Body mass changes

Body mass changes in animals that were recaptured were negative during the mating periods (March–April, Fig. 2). Data on females that had just laid their eggs were not included. During the rest of the year body mass remained constant in females, while males revealed no or a slightly negative body mass change (with one exception). To be able to use data on all captured animals, masses were converted to a size-independent condition index ($BM/(SVL)^3$, Laurie 1990). Female condition dropped to minimum levels in May/June, while the condition of males reached lowest values from March onwards (Fig. 3). Both female and male condition recovered during the period June–August, after the early rains.

Body mass relative to SVL did not differ significantly between the sexes outside the mating period (ANCOVA, see Table 3). During the mating season, however, females were significantly heavier than males. Females with SVL of 29 cm (average length of gravid females) were 20% heavier than males having the same SVL. In the nonmating season females were only slightly, but significantly, heavier than females during the mating period. Males outside the mating period were much heavier compared to males during the mating period.

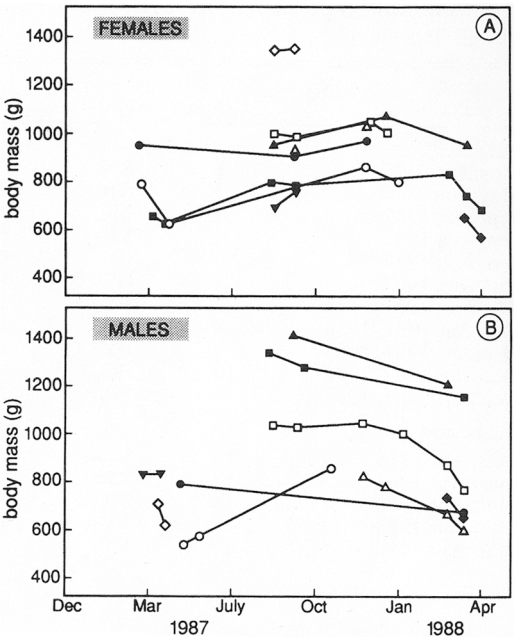

FIG. 2. Body mass of recaptured female (A) and male (B) green iguanas at the study site in the course of 1987/1988.

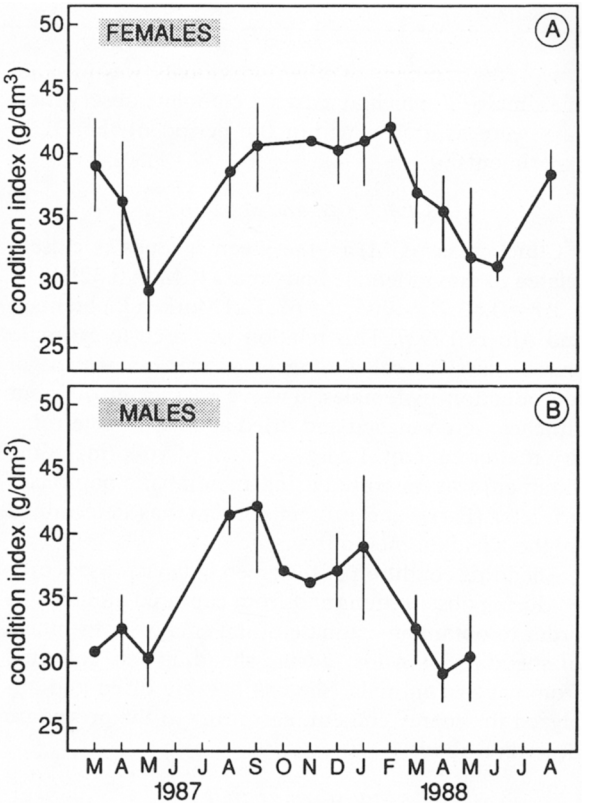

FIG. 3. Condition index ($BM/(SVL)^3$) of females (A) and males (B) from March 1987 until April 1988. Data are means ± 1 SD.

TABLE 3. Linear regression between log body mass (BM) and log snout–vent length (SVL) for males and females in the mating period (MP) and the nonmating period (NMP). The relation is described by: log(BM) = $a + b \cdot$log(SVL).*

	a	b	n	r	P
Mating period					
Males	−1.111	2.727	22	0.94	.0001
Females	−1.981	3.376	24	0.89	.0001
Nonmating period					
Males	−1.488	3.057	12	0.83	.0009
Females	−0.677	2.496	30	0.80	.0001

		ANCOVA P (slope)	P (intercept)
MP	Male vs. female	NS	.0001
NMP	Male vs. female	NS	NS
Males	RP vs. NRP	NS	.0001
Females	RP vs. NRP	NS	.05

* Slopes were not significantly different. Results of ANCOVA tests for heterogeneity of means around the regression slopes are shown in lower part of table.

Time budget

The green iguanas spent the hours between sunset and sunrise asleep on steep walls, on branches, or in crevices. After local sunrise (half an hour after sunrise) the animals moved to a basking place and assumed a basking posture. Much variation existed in the time of the day the green iguanas started basking. Basking was the major stationary activity (Fig. 4) and often took place in the company of other individuals. Resting and basking together amounted to 91% (mating period) or 93% (nonmating period) of the daytime in males and 94–96% in females. Major activities linked to locomotion consisted of foraging, and moving to and from basking and sleeping sites. There was a considerable day-to-day variation in time devoted to different activities even under stable environmental conditions. Locomotor activities of male LB during the mating period varied from 3–66 min/d in 16 consecutive days. This underlines the importance of large sample sizes per individual animal.

Locomotion.—The iguanas showed an intermittent walk; locomotor activity can be subdivided into walk bouts and resting bouts. Mean distance per walk bout was 1.4 ± 0.1 m (n = 111), and was done in 5.7 ± 0.4 steps, taking 9.9 ± 0.6 s. Mean speed amounted to 8.7 m/min. The mean resting period lasted 36.6 ± 2.1 s (n = 74). The relation between walk bout (T_w, in seconds) and distance (D, in metres) covered was: $T_w = 4.80D + 3.02$ (n = 111, r^2 = 0.443, $P < .005$). The relation between the resting bout (T_r, in seconds) and the duration of the walking bout is, $T_r = 1.12T_w + 25.81$ (n = 74, r^2 = 0.284, $P < .05$). These two equations were used to determine the time spent walking (T_w) and the time spent on locomotor activity ($T_w + T_r$) from the covered distances that were recorded during the observations (see *Methods*).

Differences between sexes and seasons.—In the mating period there were pronounced behavioral differences between males and females. Males spent more time on interactions, on locomotion, and in the vegetation (Table 4). There were no differences in time spent foraging and distance covered in the vegetation. Outside the mating period the time devoted to social activities did not differ between males and females. Bobbing frequencies, also indicating social activities (Distel and Veazey 1982), were significantly higher in males compared to females. Foraging did not occur every day. In the mating period, foraging was observed on 42% (females) and 87% (males) of the days. Outside the mating season these values are 83% (females) and 73% (males).

In the mating period males spent on average 12.4 min on social activities, more than 12 times the daily mean during the rest of the year. Females were also significantly more engaged in social activities during the mating season. There were no differences in time devoted to the various other activities between the mating season and the nonmating season in both males and females (Table 4). In summary: males were more active than females, especially so during the mating

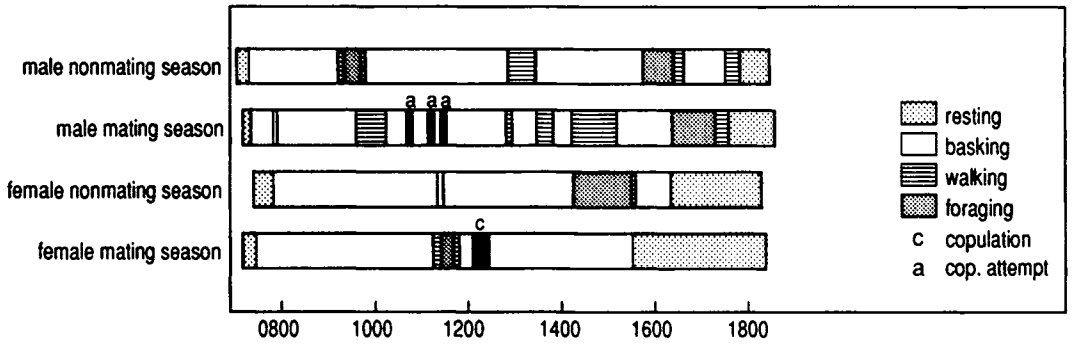

FIG. 4. Sample records of resting, basking, walking, foraging, and copulation activities of males and females in mating and nonmating seasons. Results based on 5-min intervals. Note that locomotor activity here is not identical to the actual time spent on locomotion, but based on registered locomotor activity in each 5-min interval. Observation periods from local sunrise (half an hour after sunrise) until sunset.

TABLE 4. Behavioral data of male and female green iguanas in the mating period (MP) and outside the mating period (NMP). Values are means ± 1 SE. Results (*P* values) of unpaired one-tailed *t* tests are presented below.

	No. animals	No. days	Time (min/d)			
			Interactions	Locomotor activity*	Active on rock†	In vegetation
Males NMP	3	33	0.9 ± 0.2	23.1 ± 2.6	14.1 ± 3.2	24.3 ± 2.8
Males MP	5	45	12.4 ± 2.0	24.2 ± 4.2	17.5 ± 3.4	40.1 ± 6.9
Females NMP	4	58	1.2 ± 0.7	13.6 ± 1.5	6.4 ± 1.5	29.2 ± 11.5
Females MP	4	29	3.2 ± 0.6	12.6 ± 4.7	7.2 ± 2.7	16.6 ± 7.2
Males NMP vs. MP			$P < .005$	NS	NS	NS
Females NMP vs. MP			$P < .05$	NS	NS	NS
NMP Males vs. Females			NS	$P < .01$	$P < .05$	NS
MP Males vs. Females			$P < .005$	$P < .05$	$P < .05$	$P < .05$

* Including rest bouts.
† Locomotor activities linked to foraging excluded; rest bouts included.

season. The significant differences between the seasons were restricted to social interactions.

Although the time devoted to foraging did not differ between the sexes, males in the mating season spent more time in the vegetation. Time spent foraging was significantly positively related to time spent in the vegetation in males and females, in both seasons (Fig. 5). No significant differences between the relations of males in the NMP, females in the NMP, and females in the MP existed (ANCOVA). However, the regression line of males in the mating season differed significantly in slope, revealing that the percentage foraging of total time in vegetation was lower. During the mating season males tend to accompany foraging females. Because most groups consisted of one male and two to three females, the time males spent in the vegetation was relatively long. In the vicinity of grazing females, males showed an increase of bob displays. Bob frequencies of males in the vegetation during the mating season were significantly higher than those of males outside the mating season (0.35 ± 0.19 bobs per minute, n = 16, compared to 0.13 ± 0.11 bobs per minute, n = 16).

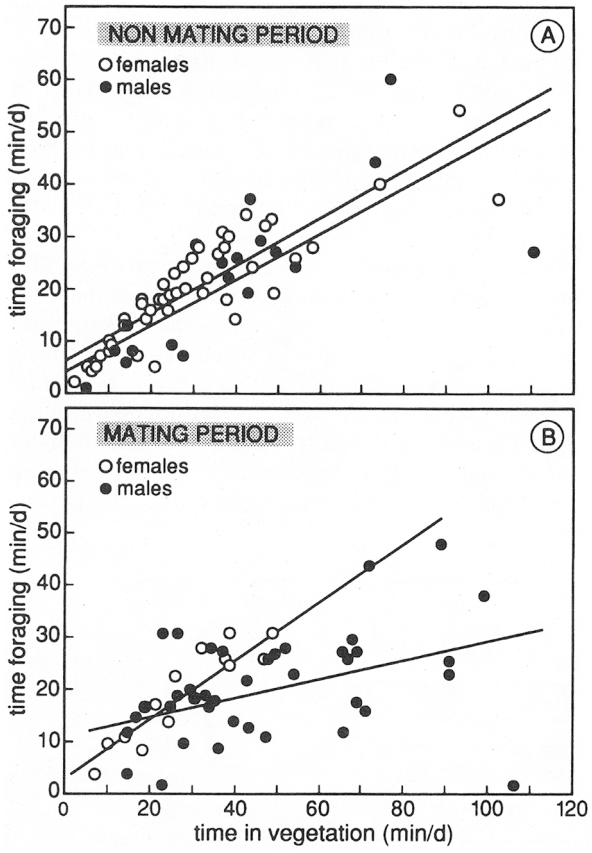

FIG. 5. Time spent on foraging in relation to the time spent in vegetation in males and females in the nonmating period (A) and the mating period (B). Equations: females NMP: y = 6.02 + 0.45x, r = 0.87, $P < .0001$; males NMP: y = 3.88 + 0.44x, r = 0.77, $P < .0001$; females MP: y = 2.79 + 0.60x, r = 0.91, $P < .0001$; males MP: y = 11.13 + 0.18x, r = 0.45, $P < .01$.

SMR and RMR. The relation between body temperature (T_b) and metabolic rate is described by exponential functions (Schmidt-Nielsen 1983). The equation of the standard metabolic rate (SMR) in our study is:

$$\log VO_2 = -2.5212 + 0.038T_b$$
$$(r = 0.987, P < .001, n = 6).$$

VO_2, the O_2 consumption rate, is expressed in millilitres per gram per hour. The slope of the SMR corresponds to a Q_{10} of 2.40. Resting metabolic rate (RMR) differs significantly (ANCOVA) from the SMR and is described by:

$$\log VO_2 = -2.3406 + 0.0362T_b$$
$$(r = 0.975, P < .001, n = 8),$$

with a Q_{10} of 2.30.

Mean body temperatures (T_b), standard metabolic rates (SMR), and heat increment in feeding (HIF = RMR − SMR) of the animals for which DEE and field body temperatures were obtained are presented in Table 5. SMR at night amounted to 10–16% of the daily energy expenditure as determined by the DLW meth-

TABLE 4. Continued.

Time (min/d)		Distance traveled (m/d)		Bob frequency (no./min)
Meal	Foraging	Rock	Vegetation	
17.9 ± 2.9	14.3 ± 6.1	57.9 ± 6.0	19.3 ± 3.7	0.34 ± 0.06
24.3 ± 2.8	15.2 ± 0.8	59.2 ± 8.2	19.5 ± 2.4	0.33 ± 0.05
23.6 ± 8.4	16.0 ± 4.2	34.4 ± 3.4	15.3 ± 6.4	0.04 ± 0.01
14.8 ± 6.5	11.5 ± 4.9	28.2 ± 10.1	18.3 ± 8.3	0.07 ± 0.07
NS	NS	NS	NS	NS
NS	NS	NS	NS	NS
NS	NS	$P < .01$	NS	$P < .001$
NS	NS	$P < .05$	NS	$P < .001$

od; SMR (day) amounted to 17–26%. The heat increment of feeding (RMR − SMR) at night was 4–5% and during daytime 6–8% of DEE. On average 45–64% of the DEE were costs above RMR.

Metabolizable energy intake

Metabolizable energy intake in the mating season (March–April) was low compared to the rest of the year in both sexes (Table 6). The difference in MEI between MP and NMP was significant (t test) when data from both sexes were lumped. There was much variation in the daily MEI within and between individual green iguanas (Fig. 6). This shows that for a reliable estimate of the mean MEI, data on food intake of several days are necessary. From the 17 green iguanas for which DEE has been measured, daily food intake via direct observations covering at least 6 d has been obtained in eight animals (Table 7). Almost all animals were in negative energy and mass balance. In many cases MEI could not cover the requirements and energy reserves were probably drawn upon, as is indicated by the relation between MEI and body mass changes (Fig. 7). To make an estimation of DEE from MEI and body mass loss it was assumed that 70% of the body mass loss was water, and the remaining 30% was tissue that had been used as an energy source. This could have been fat as well as proteins. The amount of fat (body) reserves of the animals under study is not known. By calculating DEE from MEI plus fat metabolism (energy gained from fat metabolism equals 39.7 kJ/g), a maximal estimate of DEE is obtained. These values indicate that fat stores may have accounted for the difference between MEI and DEE measured by the DLW method (Table 7).

Energetic needs for clutch formation

The dry mass (DM) of the eggs from the green iguanas (shell included) averaged 4.71 ± 1.29 g (n = 12) per egg. The eggs contained 68.4 ± 3.0% H_2O (n = 12), the protein content was 45.3 ± 7.1% of DM (n = 10), and the energy content of that DM amounted to 26.05 ± 0.92 kJ/g (n = 6). The amount of metabolizable energy needed to cover the demand for one clutch can be calculated, once the energy requirements of egg production are known. Since most of the egg synthesis takes place in the last part of the period of vitellogenesis

TABLE 5. Daily energy budgets for green iguanas, derived from time budgets and body temperatures.* Energy expenditure is expressed in $kJ \cdot kg^{-1} \cdot d^{-1}$.

				Calculated from relations with T_b										
				T_b (°C)		SMR		HIF						
Period	Iguana	Sex	BM (g)	Day	Night	Day	Night	Day	Night	RMR (24 h)	Locomotion costs	DEE	DEE/RMR	DEE/SMR
AS87	GO	♀	1328	35.6	29.3	14.6	8.6	4.6	3.0	30.8	9.9	55.6	1.8	2.4
DJ87, 88	BG	♀	902	34.7	29.3	13.8	9.9	4.4	3.5	31.5	7.6	64.1	2.0	2.7
MA88	LL	♀	783	32.8	27.2	13.2	7.6	4.4	2.8	27.9	17.9	65.9	2.4	3.2
MA88	PB	♂	628	33.3	27.2	14.5	8.4	4.7	3.0	30.7	24.1	85.7	2.8	3.7
MA88	LB	♂	695	33.9	27.2	15.5	8.3	5.0	3.0	31.8	26.0	77.0	2.4	3.2
MA88	LY	♂	815	32.8	27.2	13.2	7.6	4.4	2.8	28.0	13.9	70.2	2.5	3.4
Mean			859	33.9	27.9	14.1	8.4	4.6	3.0	30.1	16.6	69.7	2.3	3.1
1 SD			249	1.1	1.1	0.9	0.8	0.2	0.3	1.7	7.5	10.5	0.4	0.5

* Given are mean body mass (BM), and mean day and night body temperatures (T_b). Standard metabolic rate (SMR), heat increment of feeding (HIF), and resting metabolic rate (RMR) were calculated using the relations between T_b and metabolic rate (see *Results*). Costs of locomotion were obtained from the relation between daily distance covered and daily energy expenditure (DEE; see *Discussion*). For comparison the DEE (by DLW method), DEE/RMR, and DEE/SMR are presented.

TABLE 6. Mean metabolizable energy intake (MEI) for females and males from January 1987–April 1988.

Period	MEI ($kJ \cdot kg^{-1} \cdot d^{-1}$)					
	Females			Males		
	Mean ± 1 SD	No. inds.	No. days	Mean ± 1 SD	No. inds.	No. days
Jan–Feb 1987	41.7 ± 39.4	4	4			
Mar–May 1987	27.0 ± 19.6	4	20	31.2 ± 9.5	4	27
Jun–Jul 1987	30.8 ± 12.5	2	2	53.4 ± 30.4	2	6
Aug–Oct 1987	55.6 ± 4.2	3	35	40.0 ± 5.2	2	10
Nov–Dec 1987	28.1 ± 19.3	2	31	37.6 ± 14.1	2	19
Jan–Feb 1988				18.4	1	2
Mar–Apr 1988	15.9 ± 22.5	2	12	21.4 ± 6.3	3	35
NMP	40.5 ± 13.4	4		36.3 ± 9.9	4	
MP	24.0 ± 22.2	4		26.3 ± 10.3	5	

(Saint Girons 1985), it is likely that most energy needed for the egg production is obtained from stored reserves. It is assumed that efficiency of metabolic utilization is similar to birds and amounts to 85% (McDonald et al. 1981) if stored energy is converted to eggs. In that case extra energy needed for storage must be incorporated. Body fat synthesis has an efficiency of 80%. The costs then amount to: $(0.3161 \times 26.05)/(0.85 \times 0.8) = 12.11$ kJ/g. The relationship between clutch mass (CM) and BM (in grams) is: $CM = 0.32BM - 4.3$ (van Marken Lichtenbelt and Albers 1993). The costs of a 1-kg female are then 3847.3 kJ per clutch. On a yearly basis this amounts to $(3847.3 \times 100)/(365 \times 71.7) = 14.7\%$ of the annual energy expenditure.

Costs of shedding

The green iguanas shed their skin once a year. Shedding took place from July to January. In that period 44.9% of the animals inspected ($N = 98$) showed signs of shedding. In August shedding was most pronounced, when large parts of the skin were lost in 70% of the animals ($N = 20$). In the period February to June only two animals were observed showing minor signs of shedding ($N = 44$). In three captive animals all skin lost during shedding was collected. Dry skin mass amounts to 0.91% (±0.12) of live body mass. Energy content is 21.5 ± 0.31 kJ/g DM. Since DEE of an animal of 1 kg is 71.7 kJ, skin loss costs $9.1 \times 21.5/(365 \times 71.7) \times 100\% = 0.7\%$ of average DEE. If skin replacement has an efficiency of 0.75 the costs of shedding amount to 1% of the annual energy expenditure.

DISCUSSION

Energy expenditure

DEE was determined using the DLW method. In this study deuterium instead of tritiated water was used and corrections for fractionation were applied in calculating CO_2 production (Eq. 35 in Lifson and McClintock 1966). The average deviation in the DLW method in this study (2.1 ± 8.2%) falls within the range of deviations (±8%) found in other validation studies in mammals, birds, and reptiles (Congdon et al. 1978, Nagy 1980, Nagy 1983*b*, Nagy and Medica 1986). The DLW method is thus acceptable for green iguanas even in an environment with high relative humidity as met on Curaçao.

TABLE 7. Daily metabolizable energy intake (MEI) of green iguanas, and estimated daily energy expenditures (DEE) calculated from metabolizable energy intake (MEI) and body mass (BM) loss during the observation period assuming energy stored as fat. For comparison DEE (by doubly labeled water [DLW] method) is given.

Period	Animal	Sex	ΔBM (g/d)	DLW observation period (days)	MEI observation period (days)	MEI (kJ/d)	DEE estimation (kJ/d)	
							From MEI plus BM loss	By DLW method
Non-mating period								
AS87	GO	♀	0.27	22	22	66.7	...	73.9
DJ87/88	BY	♀	−1.40	22	6	42.4	59.0	59.5
DJ87/88	BG	♀	−4.44	23	22	11.7	64.6	57.8
DJ87/88	RB	♂	1.64	19	15	30.7	...	48.1
Mating period								
MA88	LL	♀	−4.63	20	7	30.2	85.4	51.6
MA88	PB	♂	−5.84	17	7	12.7	82.2	53.8
MA88	LB	♂	−5.09	16	16	21.3	82.0	53.5
MA88	LY	♂	−8.48	15	7	11.7	112.7	57.1

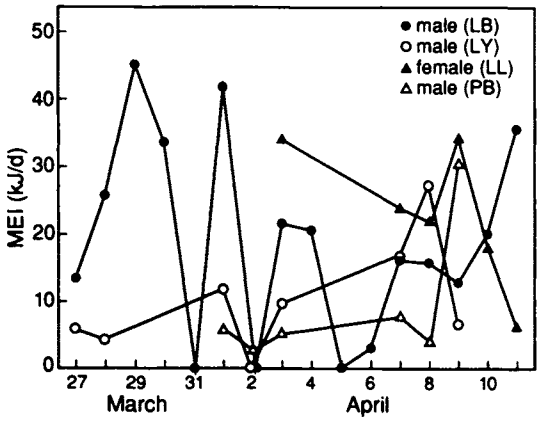

FIG. 6. Day-to-day variation in metabolizable energy intake (MEI) in four iguanas in the period from 27 March until 11 April.

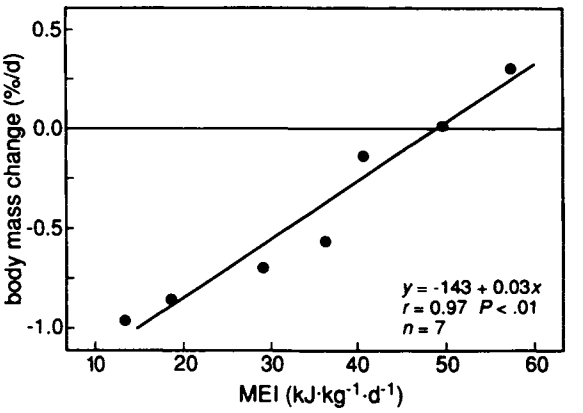

FIG. 7. Body mass changes per day, deduced from differences in body mass at recapture, plotted against metabolizable energy intake (MEI).

Daily energy expenditure of the green iguana on Curaçao was on average 71.7 ± 9.7 kJ·kg^{-1}d^{-1} (n = 16). The relation between DEE and body mass in green iguanas is not significantly different (ANOVA) from the relation for adult marine iguanas (*Amblyrhynchus cristatus*), the two being iguanines with comparable body mass (Nagy and Shoemaker 1984) (Fig. 1). Nagy (1982) provided an allometric relationship between DEE and body mass for Iguanidae (DEE = 0.224BM$^{0.80}$, R = 0.99, BM in grams). Most lizards included weighed <100 g (Fig. 8). DEE data for the green iguanas from Curaçao fit very well in this relation, stressing the predictive power of the equation including large Iguaninae.

On average DEE was 1.8–2.8 times RMR (Table 5). This is slightly higher than found in other iguanines of comparable size (*Amblyrhynchus cristatus*: 1.7, Nagy and Shoemaker 1984; *Sauromalus obesus*: 1.7, Nagy and Shoemaker 1975), but near values found in *Sceloporus occidentalis* (2.0–2.5, Bennett and Nagy 1977) and summer-active lizards (2.0–2.5, Congdon et al. 1982), and lower than in the widely foraging lizard *Sceloporus virgatus* (4.6, Merker and Nagy 1984).

The way RMR is measured may vary. Strictly speaking measurements should be taken during the natural resting phase after the metabolic rate reaches a steady state. Our data indicate that in green iguanas it takes several hours before the CO_2 production is stable. Moberly (1968*a*) found RMR's in the green iguana ≈1.4 times higher than we did, but he measured during daytime (equation from Moberly: Log VO_2 = −2.101 + 0.034T_b). Other reasons for this difference might be variations in heat increment of feeding, due to the use of different kinds of food, or taking shorter intervals between feeding and measuring. Heat increment of feeding starts during feeding, shows highest respiratory exchange shortly after feeding, and than gradually decreases. Notwithstanding these possible differences in measurements, the Q_{10} (2.24) found by us is in close agreement to Moberly's value of Q_{10} (2.29).

Time–energy budget

The energy expenditure above RMR is allocated between activities involving locomotion, and stationary activities, like basking. Although time spent on locomotion is only a fraction of the total daytime, the costs of locomotion may amount to a substantial portion of the daily energy expenditure, as will be shown below.

Costs of locomotion.—Costs of locomotion can be estimated in the following ways:

1) Gleeson (1979) provides a general formula for the costs of locomotion for quadruped lizards (costs of transport [as O_2 consumption] = 3.77BM$^{-0.25}$ mL·g^{-1}·km^{-1}, BM in grams). According to this formula locomotion would require 670 mL·kg^{-1}·km^{-1}, or 13.4 kJ·kg^{-1}·km^{-1} (conversion factor: 21.7 J/mL CO_2 production, RQ = 0.92).

2) Data from treadmill experiments (Moberly 1968*b*) reveal an oxygen consumption of 1.9 mL·g^{-1}·km^{-1} at

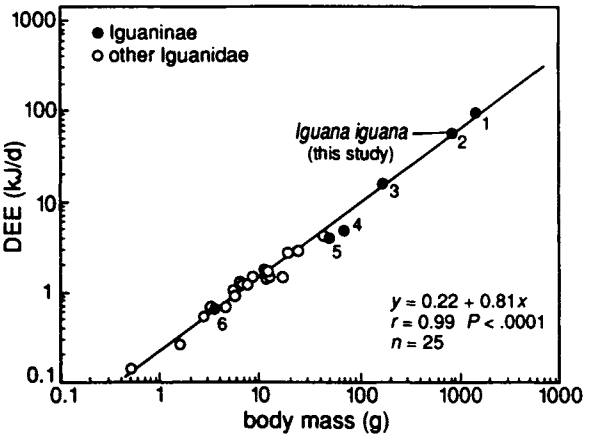

FIG. 8. Daily energy expenditure (DEE) in relation to body mass in Iguanidae. Data from Nagy (1982) and for the green iguana (*Iguana iguana*; this study). Iguanines are identified as follows: (1) *Amblyrhynchus cristatus*; (2) *Iguana iguana*; (3) *Sauromalus obesus*; (4) *Amblyrhynchus cristatus* (juvenile); (5) *Dipsosaurus dorsalis*; (6) *Dipsosaurus dorsalis* (juvenile).

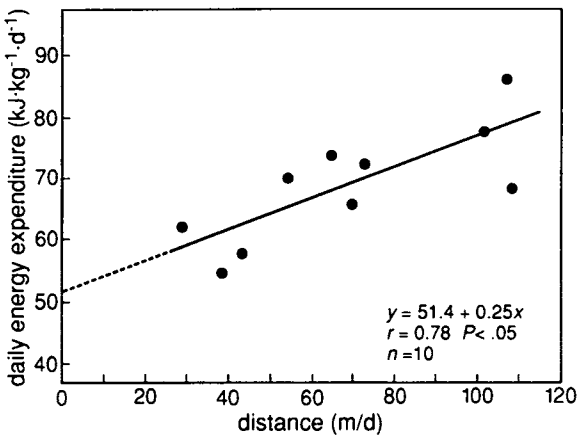

FIG. 9. Relation between the daily energy expenditure and the total distance (at any angle from horizontal to vertical) covered per day for the green iguana on the study site.

a speed of 2.2 m/min, with only small amounts of lactic acid production. This is equivalent to an energy expenditure of 37.9 $kJ \cdot kg^{-1} \cdot km^{-1}$. Field costs according to this estimate may be lower, because at higher speed, costs of transport per unit distance are lower, but blood lactate levels are higher (Moberly 1968*b*). In the field we observed a mean walking speed of 8.7 m/min. Under natural circumstances green iguanas walk in short bouts and then rest for a relatively long period. This has also been observed in *Amblyrhynchus cristatus* (Gleeson 1979) and in *Conolophus subcristatus* (Werner 1983). In this way they probably minimize anaerobic metabolism. The energy expenditure from Moberly's data is 2.8 times the outcome of the equation provided by Gleeson (1979). This discrepancy could be due to less economical locomotion in green iguanas compared to other lizards, as suggested by Gleeson (1979). However, differences in methods cannot be precluded and differences in aerobic or anaerobic capacity may also play a role.

3) By combining the results of simultaneous measurements of DEE (by the DLW method) and locomotor activity, an estimate of the costs of activities linked to transport in the field can be obtained. The daily energy expenditure is significantly related to the daily distance covered (Fig. 9). Costs of locomotion can be obtained from the slope of the relation and amount to 255 $kJ \cdot kg^{-1} \cdot km^{-1}$. The costs of locomotion as described under (1) are 6.0%, and under (2) 16.8% of the costs of locomotion as obtained from the relation DEE vs. distance. This large discrepancy is probably caused by differences in kind of locomotion. The treadmill experiments reveal costs of walking on a horizontal even surface. Green iguanas on Curaçao walk for ≈45% of the total distance on horizontal to moderate sloping irregular rock surface, whereas 25% of the distance is covered climbing up and down steep slopes and vertical escarpments. The remaining distance (30%) is made in shrubs and trees, mostly while foraging, and consists to a large extent of climbing and acrobatics on bending twigs. Treadmill experiments thus provide an estimate close to the minimum costs of locomotion and underestimate the costs of locomotor activity in the field. There is no literature available on costs of climbing in reptiles. In human beings it is known that the costs of walking up and down stairs are 11 times as high as the costs of walking horizontally (Åstrand and Rodahl 1986), which is in the same order of magnitude as the difference between costs of horizontal walking and field costs of locomotion in iguanas.

The relation between DEE and distance still leaves 22% ($r = 0.78$) of the variation unexplained. This may be due to individual differences in the allocation of climbing, horizontal walk, and locomotor activity in the vegetation. When distances covered on flat to moderately sloping rock, and distances climbing and moving in the vegetation, are treated as separate variables, multiple regression does not improve the fit ($r = 0.79$) (Table 8). Another explanation could be individual variation in the contribution of other activities linked to locomotion, like grazing (snapping and swallowing

TABLE 8. Multiple regression analyses of daily energy expenditures (DEE, in $kJ \cdot kg^{-1} \cdot d^{-1}$) in relation to covered distances (in m/d), where D = total distance; C = climbing rock; V = in vegetation; $CV = C + V$; RH = rock "horizontal"), social activity (bob frequency, [in bobs/min]), and foraging activity (number of Bites per day).*

Variables	Equations	r	P
C	NS		
V	NS		
Bob	NS		
Bite	NS		
CV	$DEE = 0.29CV + 58.0$	0.65	.042
D	$DEE = 0.25D + 51.4$	0.78	.008
RH, C, V	NS		
RH, CV	$DEE = 0.38RH - 0.19CV + 49.8$	0.79	.031
D, Bob	$DEE = 0.27D - 2.9$ Bob $+ 50.5$	0.80	.045
D, Bite	$DEE = 0.26D - 0.08$ Bite $+ 58.6$	0.95	.003
RH, CV, Bob	NS		
RH, CV, Bite	$DEE = 0.19RH + 0.31CV - 0.88$ Bite $+ 60.5$	0.91	.011
RH, CV, Bob, Bite	$DEE = 0.21RH - 0.42CV - 29.9$ Bob $- 0.12$ Bite $+ 65.0$	0.96	.017

* Note that most of the variation is explained by combining locomotor activities with social and grazing activities (see last two equations). ($n = 10$; except for bob frequencies, $n = 9$.)

food items) and social interactions (e.g., bobbing). Multiple regression between DEE and distances covered per day (horizontal and climbing/vegetation walks separated again), bob frequency, and number of bites per day explains up to 96% of the variation (Table 8). This demonstrates that our time budget may provide reliable estimates for DEE if the costs of the various activities, particularly the costs of climbing, are known. Finally, part of the variation can be caused by differences in body temperature, since costs of locomotion are positively related to body temperature in the desert lizard *Dipsosaurus dorsalis* (John-Alder and Bennett 1981, Bennett 1982), though in green iguanas no relation between body temperature and the energy costs of walking was found (Moberly 1968*b*).

Although the estimates of costs of locomotion in the green iguana are to some extent influenced by foraging costs other than those of transport, and social activities linked to locomotion, they provide a field estimation of the allocation of the energy expended above RMR, a point hardly explored as yet in reptiles.

Stationary activities.—The energy expenditure above RMR plus costs of locomotion amounts to an average of 33% of DEE. This part of the DEE may be partly accounted for by the costs of (social) activities, cardiovasculatory adjustments during basking, and/or nasal gland secretion. As mentioned above, the actual heat increment of feeding may have been somewhat higher than the measured HIF. Costs of detoxifying and/or eliminating toxic chemicals in the food may also account for a part of the DEE above RMR. The major part of the costs above RMR and costs of locomotion, however, were probably costs linked to maintaining posture during locomotion and basking. Nagy and Shoemaker (1984) found in the Galápagos marine iguana, *Amblyrhynchus cristatus,* that the costs in addition to RMR and locomotion constitute 37% of the DEE, which is in close agreement to our value of 33%. They also allocate much of these costs to postural costs of basking. Experiments on treadmills in mammals reveal that linear extrapolation of the rate of oxygen consumption at zero speed (the Y intercept) is 1.5–2.0 times resting levels and is assumed to be associated with postural adjustments associated with the active animal (Schmidt-Nielsen 1972, 1983). Extrapolation of the DEE at zero speed in the green iguana (Fig. 9) amounts to 52 $kJ \cdot kg^{-1} \cdot d^{-1}$. Mean RMR is 30 $kJ \cdot kg^{-1} \cdot d^{-1}$; hence the resting animal while immobile expends 22 kJ above RMR. Assuming that postural adjustments occur during daytime only, the extra costs are 1.16 times RMR (mean daytime RMR = 19 $kJ \cdot kg^{-1} \cdot d^{-1}$). This is in agreement with the costs of postural adjustments (1–2 times RMR) as can be calculated from the data from Gleeson (1979) in *Amblyrhynchus cristatus* and *Conolophus subcristatus,* relying on values reported for RMR and the relation between metabolic rate and walking speed. The estimates presented above of the various cost factors in green iguanas reveal that on average SMR amounted to 33% (range: 27–42%), heat increment of feeding to 11% (range: 9–14%) of the DEE, while costs involving locomotion made up 23% (range: 11–34%) and postural adjustments plus other costs were 33% (range: 27–40%) of the daily energy expenditure.

Energy allocation.—DEE between males and females was not significantly different, although DEE in the mating period tended to be larger in males. When the costs of clutch production are added to the measured DEE in females, energy expenditure still did not differ significantly from DEE of males, indicating a similar annual level of energy expenditure in males and females. For the animals for which activity data, body temperatures, and DEE (by doubly labeled water method) are available (Table 5), the energy allocation is presented in Fig. 10, using the above-described calculations. Comparisons between the sexes reveal that DEE in males tended to be higher than DEE in females, which can be explained by differences in activities linked to locomotion and postural adjustments. Small differences in time devoted to locomotor activities have a substantial impact on the energy expenditure. While in males during the mating period, on average only 1.7% of the time was devoted to locomotion, costs of locomotion amounted to an average of 27% of the DEE. Differences between males and females in bob frequencies also indicate extra costs in males due to social or territorial activities. Females, on the other hand, produce egg clutches. We do not know the DEE of females just before egg laying, but there seem to be two phases. Initially, females save energy by remaining almost inactive, and in this period probably conversion of body reserves into egg tissue takes place, followed by a period of migration to the nesting site, with burrowing activities and egg laying. Costs of these activities may be substantial. We have indications that, indeed, gravid females in the weeks prior to migration to the nesting area spent much less time on locomotor and foraging activities. For example, a gravid female (GO) was followed on a regular basis from February to May. Out of the six observation days in March, she went foraging only one time and covered on that day 50 m. On the other days distance covered was only 3 m, to move to and from a basking spot and the sleeping place. This example adheres to the general pattern that females forage on 42% of the days in the mating period, compared to 83% outside the mating period. From 1 April onwards she was not seen any more on "her" boulder, until 30 April, after she had laid her eggs.

Daily energy expenditure and metabolizable energy intake

Body mass of the males dropped drastically in the mating period (March/April), primarily due to a decrease in MEI. In this period body mass loss in females was less severe, probably because of less locomotion activities. They reached their lowest body mass con-

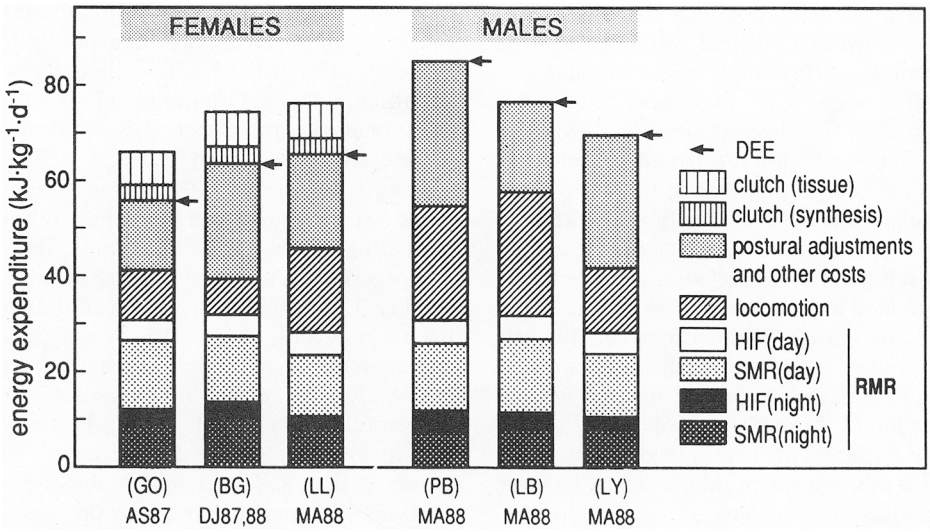

FIG. 10. Energy allocation in green iguanas during our study. Daily energy expenditure (DEE), standard metabolic rate (SMR), heat increment of feeding (HIF), costs of locomotion, and costs of postural adjustments of individual animals. Costs of egg clutch production are calculated on a yearly basis.

dition in May–June, during the time of oviposition. After the first rains in May body mass increased in both sexes due to an increase of MEI and decreased again in the beginning of the next dry season. The absolute mean MEI values were below the requirements (Table 6), but mean MEI values may be deceptive, because of large day-to-day and inter-individual differences in MEI. In addition, autumn 1987 and spring 1988 were extremely dry periods, compared to the average precipitation, resulting in a much lower food availability (van Marken Lichtenbelt 1991). Although food availability in the reproductive period was less than in the rest of the year, the animals did not devote extra time to foraging in that period. This could be due to depletion of food, extra costs of foraging, to priorities of other activities, to reduced room left in the abdomen (in females), due to room taken by the eggs (Rand 1984, and W. D. van Marken Lichtenbelt, *personal observations*), or to the water content of the food (e.g., *Sauromalus obesus* stops foraging once water content in the food drops below a certain level; Nagy 1972).

The use of fat reserves permits survival in periods of low intake. Lipid storage in lizards is often positively linked to food availability and inversely related to reproductive activity (Derickson 1976, Minnich 1971). Our data on MEI and body mass changes indicate that outside the mating period the energy deficiencies could have been replenished by fat metabolism (Table 7). In the mating period the energy expenditure estimation from MEI plus energy from fat stores exceeded DEE from DLW. This can be explained by a reduction of the gut content or by the use of protein stores as a source of energy. The animals in the mating period probably did not have fat (body) reserves left.

From 1987 until spring 1988 most animals were in negative mass balance or at best managed to maintain mass balance, in spite of the fact that most animals were not full grown. In an environment with such strong yearly differences in rainfall and food availability, green iguanas probably are able to survive in dry years because of previously stored energy reserves. A gradual decrease in body mass over a period of several years has also been observed in marine iguanas on the Galápagos islands (Laurie 1990). Clearly more data of several consecutive years on the energetics of the green iguanas will be profitable. Our data so far indicate that fluctuations in body mass in the course of the year are not a result of differences in energy expenditure, but are caused by differences in daily metabolizable energy intake. On a yearly basis energy expenditure does not differ in both sexes; however, energy allocation does. Females devote approximately 15% (plus the costs associated with oviposition) of their energy budget to the production of the eggs, while males are more heavily engaged in social activities and spend twice as much time on locomotor activities as females.

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